

REVISED CLASSIFICATION AND PHYLOGENETIC
HYPOTHESIS FOR THE
ACANTHOSTOMINAE LOOSS, 1899
(DIGENEA: OPISTHORCHIFORMES: CRYPTOAGONIMIDAE)

Daniel R. Brooks and Barbara Holcman

Abstract.—Specimens of an acanthostome digenean originally identified as *Acanthostomum scyphocephalum* and later transferred to *Timoniella* are described and named as a distinct species of *Timoniella*. *Acanthostomum scyphocephalum* sensu strictu is included in an updated phylogenetic analysis of the acanthostome digeneans. The new analysis differs from an earlier one by Brooks (1980) by allowing reversals (Wagner criterion vs. Camin-Sokal criterion), producing a more parsimonious representation of character data; no transformation series needed re-polarization. *Acanthostomum scyphocephalum* is a member of the clade containing all other species of *Acanthostomum* occurring in North, Central and South America. *Acanthostomum* is paraphyletic if *Atrophecaecum* is excluded from it; accordingly, the two genera are synonymized. No other changes from the hypothesis of Brooks (1980) resulted. The resulting annotated phylogenetic classification, with synapomorphic diagnoses, includes *Acanthostomum* as the sister-group of *Caimanicola*, *Proctocaecum* as their sister-group, the monotypic *Gymnatrema* as their sister-group, and *Timoniella* as the basal sister-group. Four new subgenera are proposed, one in *Timoniella*, one in *Proctocaecum*, and two in *Acanthostomum*.

The acanthostome digeneans (Opisthorchiformes: Cryptogonimidae: Acanthostominae) inhabit a variety of piscivorous poikilotherm amniote vertebrates throughout the tropical and subtropical regions of the world. Brooks (1980) provided the first phylogenetic systematic analysis of the acanthostomes. He recognized six genera, *Timoniella* Rebecq, 1960, *Proctocaecum* Baugh, 1957, *Gymnatrema* Morozov, 1955, *Caimanicola* Teixeira de Freitas & Lent, 1938, *Acanthostomum* Looss, 1899 and *Atrophecaecum* Bhalerao, 1940, although *Acanthostomum* had no synapomorphy to support its recognition as a monophyletic group.

Since that time, publications have described two additional species and discussed their phylogenetic relationships (Brooks & Caira 1982, Blair et al. 1988),

and have added data about host and geographic distributions, as well as valuable taxonomic information (Ostrowski de Nuñez 1984a, 1984b, 1986, 1987). This study provides a description of a new species, and incorporates the new data provided by Ostrowski de Nuñez into the phylogenetic data base for the acanthostomes, resulting in an updated phylogenetic hypothesis and an annotated classification with cladistic diagnoses for all taxa.

Methods

In addition to the material specified in Brooks (1980), Brooks & Caira (1982) and Blair et al. (1988), we have examined the following material loaned from Dr. Margarita Ostrowski de Nuñez: *Acanthostomum gnerii* (19 specimens from *Rhamdia*

sapo, Laguna Chis-Chil, Prov. Buenos Aires, Argentina); *Acanthostomum megacetabulum* (1 specimen from *Drymarchon corais melanurus*, Villahermosa, Mexico); *Caimanicola marajoarum* (14 specimens from *Crocodylus intermedius*, Caracas, Venezuela; 3 specimens from *Paleosuchus* sp., Antioquia, Colombia); *Caimanicola brauni* (13 specimens from *Phrynosoma hilarii*, Buenos Aires, Argentina); *Timoniella loossi* (3 specimens from *Crocodylus intermedius*, Caracas, Venezuela); *Acanthostomum* sp. VI of Ostrowski de Nuñez (1984b) (2 specimens from *Caiman fuscus*, Rio Chagras, Panama). All measurements are in μm unless otherwise noted. TBL = total body length. Figures were drawn with the aid of a drawing tube.

Results and Discussion

Timoniella ostrowskiae, new species

Figs. 1–3

Synonyms.—*Acanthostomum scyphocephalum* of Mañe-Garzon & Gil, 1961; *Timoniella scyphocephala* of Brooks, 1980.

Description.—(based on holotype and 2 paratypes) Body 2.98–3.15 mm long by 420–540 wide at midbody. Tegument covered with spines of uniform size. Oral sucker terminal, bell-shaped, 410–517 long by 443–517 wide, armed with single row of 23 spines 68–78 long by 20–25 wide. Pharynx 197–205 long by 187–230 wide. Prepharynx 377–426 long. Ratio of oral sucker width to pharyngeal width 1:0.42–0.45. Ceca opening separately at posterior end of body. Acetabulum 1.22–1.47 mm from anterior end; forebody 41–47% TBL. Acetabulum 140–156 long by 131–147 wide; ratio of oral sucker width to acetabulum width 1:0.27–0.32. Testes tandem, intercaecal, near posterior end of body; posttesticular space 5.2–5.5% TBL. Anterior testis 187–205 long by 123–139 wide, posterior testis 180–221 long by 115–123 wide. Male genitalia consisting of coiled external seminal vesicle lying posterodorsal to acetabulum and musculo-

glandular pars prostatica and ejaculatory duct extending anteriorly dorsal to acetabulum, opening into genital atrium. Gonotyl lacking. Genital pore ventral, medial, immediately preacetabular. Ovary 90–139 anterior to anterior margin of anterior testis, 123–139 long by 115–123 wide. Seminal receptacle posterodorsal to ovary, between ovary and anterior testis. Mehlis gland present, Laurer's canal short. Uterine loops extending posteriorly to lateral margin of anterior testis, anteriorly to posterior margin of seminal vesicle, occupying 38–43% TBL; terminal portion of uterus opening into genital atrium. Vitellaria follicular, in two longitudinal extracecal fields extending from level of posterior margin of seminal vesicle to slightly posterior to anterior margin of anterior testis. Eggs 25–27 long by 10–12 wide.

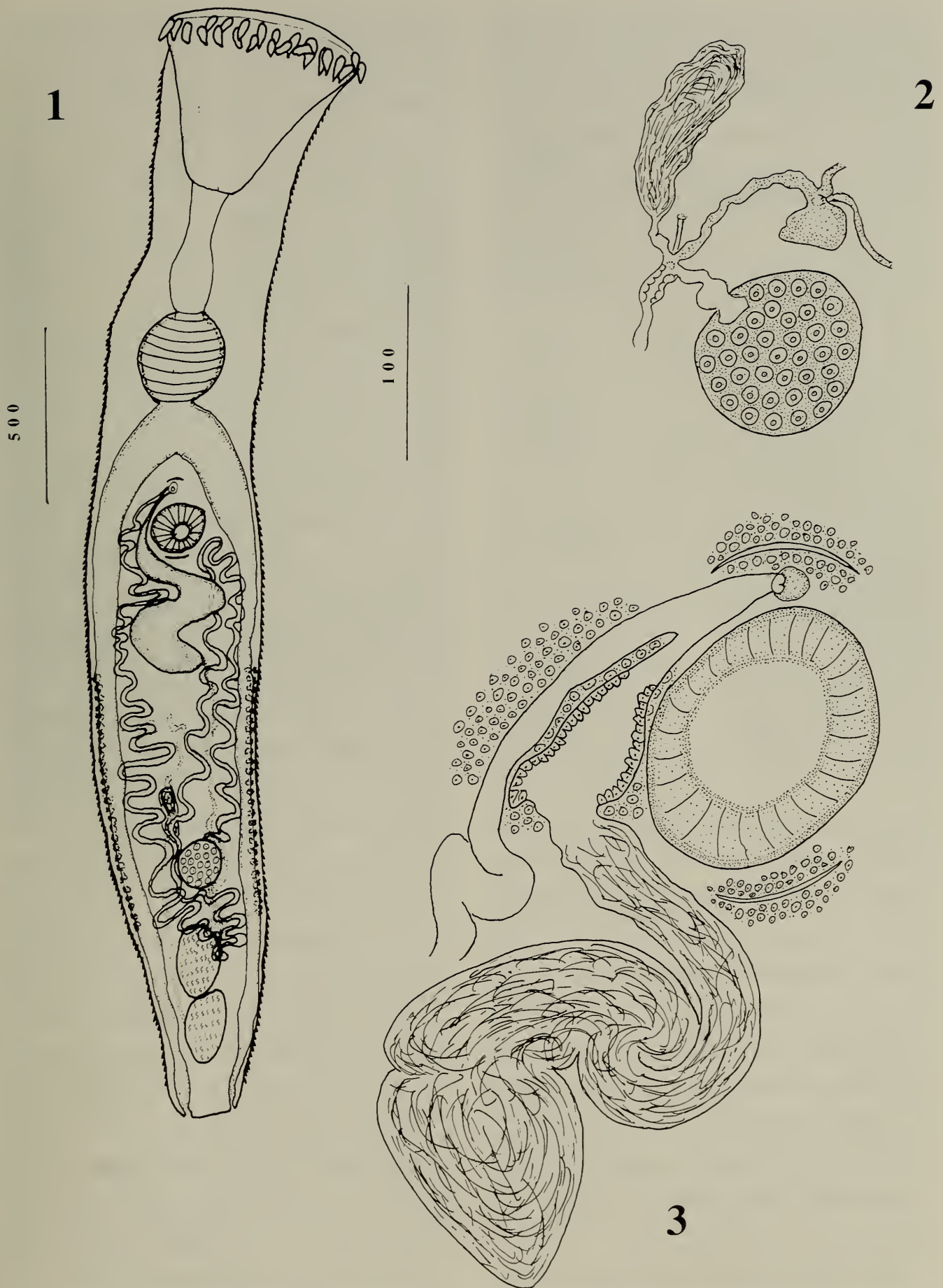
Type host.—*Phrynosoma hilarii* (Dumeril and Bibron).

Type locality.—Rio Negro, Paso de los Toros, Departamento de Tacuarembó, Uruguay.

Holotype.—URFC Helm. Coll. No. 11038. Paratypes: URFC Helm. Coll. No. 11039–11040.

Etymology.—The species is named in honor of Dr. Margarita Ostrowski de Nuñez, who first recognized its distinct identity.

Brooks (1980) was unable to locate the holotype of *A. scyphocephalum* Braun, 1899 which had been collected in "*Testudo matamata*" from southern Brazil. Based on examination of specimens collected in *Phrynosoma hilarii* from Uruguay (reported by Mañe-Garzon & Gil 1961), Brooks (1980) transferred the species to *Timoniella* because it possessed preovarian rather than postovarian seminal receptacles, a unique and unreversed synapomorphy that diagnoses *Timoniella* among the acanthostomes. Ostrowski de Nuñez (1986) found the holotype of *Acanthostomum scyphocephalum* Braun, 1899, and showed that it was a member of *Acanthostomum*. The



Figs. 1-3. *Timoniella (Maillardiella) ostrowskiae*. 1. Ventral view of holotype. 2. Ootype region. 3. Terminal genitalia.

Table 1.—Homoplasious changes for 17 characters of acanthostomes. Character consistency index = number of apomorphic states for each character divided by total number of changes postulated on the phylogenetic trees. For character identities, see Appendix 1.

Character state	Figure #-Character number on figure	Character consistency index
1-0	9-36	50% (1/2)
2-0	9-38	50% (1/2)
6-0	5-3	50% (1/2)
7-0	4-17, 5-12	50% (1/2)
9-0	8-10	
9-1	4-10, 5-1, 6-3, 7-5, 8-7, 9-32	33% (3/9)
10-0	6-1	
10-1	5-2, 7-4, 8-2, 8-17, 9-29, 9-35	17% (1/7)
11-1	5-4, 9-21	50% (1/2)
12-1	5-5, 6-11, 8-14	33% (1/3)
13-1	5-6, 6-6, 8-13, 9-22, 9-33	33% (2/6)
14-2	5-13, 6-7, 8-1	
14-3	5-14, 9-19	
14-5	4-12, 6-4, 8-6, 9-26	57% (8/14)
15-1	5-8, 8-18, 9-24	50% (2/4)
16-0	7-3	
16-1	4-20, 5-9, 6-8, 9-20, 9-28, 9-34	17% (1/7)
17-1	5-10, 8-3	67% (2/3)
18-0	8-30	
18-1	5-11, 7-1, 8-9	40% (2/5)
22-0	7-2, 8-11	50% (2/4)
23-1	6-5, 6-13, 9-25	33% (1/3)
29-1	5-15, 6-12, 8-15	50% (2/4)

specimens reported by Mañe-Garzon & Gil (1961) therefore appear to represent a previously unnamed species of *Timoniella*, which we formally described and named above. *Timoniella ostrowskiae* is most closely related to *T. incognita* Brooks, 1980, *T. loossi* (Perez Viguera, 1957) Brooks, 1980, *T. absita* Blair et al., 1988, and *T. unami* (Pelaez & Cruz, 1957) Brooks, 1980, all of which lack gonotyls. Of those species, *T. ostrowskiae* is the only one exhibiting ceca opening separately at the posterior end of the body; *T. incognita* has blindly-ending ceca, and the remaining three species have ceca opening into the excretory vesicle near the posterior end of the body.

As indicated in the introduction, new information concerning acanthostomes has accumulated since Brooks (1980) produced

the first phylogenetic systematic hypothesis for the group. Brooks (1980) used the Camin-Sokal (also known as the Weighted Invariant Step Strategy [WISS]—Wiley et al. 1991) criterion, allowing no evolutionary reversals, in producing a phylogenetic tree for the acanthostomes. He found no synapomorphy to support the monophyly of *Acanthostomum*, nor any character that could link *Acanthostomum* with either *Caimanica* or *Atrophecaecum*, two genera having synapomorphic support that were shown forming an unresolved trichotomy with *Acanthostomum*. In this study we re-analyzed the data using the less restrictive Wagner criterion (Wiley et al. 1991) after checking character polarizations using estimates of higher-level digenean phylogenetic relationships (Brooks et al. 1985, Brooks et al. 1989, Brooks & McLennan 1993) not available to Brooks (1980). We found support for the original character polarizations of Brooks (1980, see also Brooks & Caira 1982, Blair et al. 1988) but, as would be expected, we also found more parsimonious optimizations for some homoplasious characters when reversals were allowed (for a summary of transformation series, see Appendix 1; for a summary of homoplasious changes, including reversals, see Table 1). Based on the information presented by Ostrowski de Nuñez (1986), we included *Acanthostomum scyphocephalum* in the phylogenetic framework; it appears to be a member of the clade containing all the other species of *Acanthostomum* occurring in North, Central and South America (Fig. 8). Most importantly, the new analysis showed that *Acanthostomum* is paraphyletic (Fig. 8), and should be combined with *Atrophecaecum* (Figs. 8, 9).

Systematic theorists have begun investigating the problems of providing robust means for assessing the results of phylogenetic analyses (e.g., Archie 1989, Farris 1989, Sanderson & Donoghue 1989, Klassen et al. 1991, Meier et al. 1991). These studies have produced some interesting, and

in some cases initially counter-intuitive, findings. For example, the minimum significant value for the most commonly used indicator, the consistency index (CI—Wiley et al. 1991), drops as one adds taxa and characters to a study; for example, a study using 50 characters for 20 taxa and reporting a CI of 65% may actually be more robust than using 10 characters for 7 taxa and reporting a CI of 80%. This happens because there are often apomorphic character changes occurring once within a given taxon that also occur once in another taxon. If the scope of a study were expanded to include both taxa, the estimate of homoplasy would increase (and the CI would drop) even if the hypothesized phylogenetic relationships of the (now) subgroups did not change. Or, to use current terminology, we would say that a *global* phylogenetic analysis had discovered homoplasy that the two *local* analyses failed to recognize. In some cases such global homoplasy could affect the hypotheses of relationships, so recognizing global homoplasy may play an important role in determining robust character polarities during outgroup comparisons at the inception of a phylogenetic analysis (e.g., Maddison et al. 1984, Wiley et al. 1991).

The acanthostomes provide an excellent illustration of the relationship between local and global parsimony considerations in phylogenetic analysis. If we treat all the acanthostomes as a single taxon, the consistency index for the characters reported herein is 50.5% (49 apomorphic character states and 97 character changes). This value is low for digeneans in general, the consistency index based on global parsimony considerations for all digeneans being approximately 72% (Brooks & McLennan 1993). By contrast, if we treat each of the clades denoted as a genus separately, the estimated homoplasy is generally much lower (100% for the characters used at the generic level by themselves, including the monotypic *Gymnatrema*, for the species of *Timoniella*, and for the species of *Caimanicola*, and

84.6% for the species of *Proctocaecum*), the exception being *Acanthostomum*, for which the consistency index based on local parsimony considerations is 51%. This means that although there is much homoplasy among the acanthostomes as a whole, most of it is dispersed among clades rather than concentrated within clades. Thus, determination of plesiomorphic states by outgroup comparisons is not problematical, and there is presently a single most parsimonious tree, for the group.

Mensural, or continuous variable, characters are problematical for phylogenetic reconstruction. The determination of discrete character states is often problematical for such traits; options seem to range from considering almost every species autapomorphic to recognizing very few states and there is no consensus approach among phylogeneticists. Brooks (1980) adopted a conservative approach to recognizing character states based on his examination of available specimens. Taking a conservative approach to such traits often results in considerable homoplasy. In the present study, the homoplasy is distributed among half (17 of 34) of the transformation series (1, 2, 6, 7, 9–18, 22–23, and 29 in Appendix 1), 9 of which (10, 12–13, 15–18, 22–23) are mensural in nature. Of the 48 homoplasious character transformations, 28 (58.3%) stem from the mensural characters and 20 (41.7%) from the qualitative traits; moreover, the mensural traits that show homoplasy have a combined character consistency index of 28.6% (14/42), while the qualitative traits that show homoplasy have a combined character consistency index of 48.7% (19/39) (Table 1). While suggestive, these data are actually moot with respect to the question of whether or not such characters provide adequate phylogenetic information, because they exhibit high levels of homoplasy but do not support relationships that are contradicted by non-mensural characters. A strong test of these characters requires a search for intrinsically qualitative

characters whose apomorphic states support phylogenetic relationships that conflict with the ones supported by the present data base.

Conclusions

The changes discussed above are reflected in the phylogenetic trees, cladistic diagnoses, and classification below (the monotypic *Gymnatrema* has no separate cladogram). In the following, italicized numbers refer to synapomorphies listed by number on Fig. 4; other numbers refer to synapomorphies listed by number on Figs. 5–8. Four new subgenera are proposed. Each is named for a digenean systematist who has advanced our understanding of acanthostome relationships: Dr. Claude Maillard, University of Montpellier, France; Dr. David Gibson, British Museum (Natural History), London, England; Dr. David Blair, James Cook University, Townsville, Australia; and Dr. Robin Overstreet, Gulf Coast Marine Research Laboratory, Ocean Springs, Mississippi, USA.

Subfamily Acanthostominae Poche, 1926 (Fig. 4)

Diagnosis.—Cryptogonimidae with terminal oral sucker (1); armed with single row of spines (2); preacetabular pit (3); genital pore not in preacetabular pit (4); seminal vesicle coiled posteriorly (5); suckerlike gonotyl present (6).

Genus *Timoniella* Rebecq, 1960 (Fig. 5)

Diagnosis.—Acanthostominae preovarian seminal receptacle (7).

Subgenus *Timoniella* Rebecq, 1960

Diagnosis.—*Timoniella* having vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (1); length of body occupied by uterine loops more than 50% TBL* (2); seminal vesicle not coiled

posteriorly* (3); prepharynx shorter than pharynx* (4); ratio of oral sucker width to pharyngeal width 1:0.25–0.40* (5); ratio of body length to width averaging 7.5–15:1* (6).

T. praeterita (Looss, 1901) Maillard, 1974

Diagnosis.—Cyclocoel (7); forebody 10–20% TBL* (8); maximum body length 7–16 mm* (9).

T. imbutiformis (Molin, 1859) Brooks, 1980

Diagnosis.—Ratio of oral sucker : acetabular width 1:0.8–1.3* (10); oral spines averaging 25–30 in number* (11).

Subgenus *Maillardiella*, new subgenus

Diagnosis.—*Timoniella* lacking gonotyls* (12).

T. incognita Brooks, 1980

Diagnosis.—With characters of the subgenus.

Remarks: This species was originally reported by Nasir (1974) as *Acanthostomum scyphocephalum* inhabiting *Caiman crocodilus crocodilus*. According to Ostrowski de Nuñez (1984b), the acanthostomes reported as *Acanthostomum scyphocephalum* from *Drymarchon corais* by Nasir (1974) may be a still undescribed species.

T. ostrowskiae Brooks & Holcman, 1993

Diagnosis.—Ceca opening separately at posterior end of body* (13).

T. unami (Pelaez & Cruz, 1957) Brooks, 1980

Diagnosis.—Ceca opening into excretory vesicle* (14); vitelline follicles extending posteriorly to middle of posterior testis* (15).

T. loossi (Perez Vigueras, 1957) Brooks, 1980

Diagnosis.—Ceca opening into excretory vesicle* (14); vitelline follicles extending

posteriorly to middle of posterior testis* (15); vitelline follicles confluent dorsally (16).

T. absita Blair et al., 1988

Diagnosis. — Ceca opening into excretory vesicle* (14); vitelline follicles extending posteriorly to middle of posterior testis* (15); constriction in seminal vesicle (17).

Genus *Gymnatrema* Morozov, 1955

Diagnosis. — Acanthostominae having some uterine loops lateral to testes but none posttesticular (8); vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (10); vitelline follicles confluent posttesticularly (11); one cecum atrophied* (12); one cecum opening laterally and one cecum ending blindly (13).

G. gymnarchi (Dollfus, 1950) Morozov, 1955

Diagnosis. — With characters of the genus.

Genus *Proctocaecum* Baugh, 1957

(Fig. 6)

Diagnosis. — Acanthostominae having some uterine loops lateral to testes but none posttesticular (8); ceca opening separately and laterally at even levels (9); excretory vesicle Y-shaped with short stem and constriction of arms in middle (14); eggs averaging more than 30 μm long (15); gonotyl large, solid-muscular (16).

Subgenus *Proctocaecum* Baugh, 1957

Diagnosis. — *Proctocaecum* having relative length of uterine loops less than 45% TBL* (1).

P. gonotyl (Dollfus, 1950) Brooks, 1980

Diagnosis. — With characters of the subgenus.

P. vicinum (Odhner, 1902) Brooks, 1980

Diagnosis. — Ceca opening separately and laterally at uneven levels (2).

P. coronarium (Cobbold, 1861) Brooks, 1980

Diagnosis. — Ceca opening separately and laterally at uneven levels (2); vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (3); one cecum atrophied* (4); maximum oral spine length more than 100 μm * (5).

Subgenus *Overstreetium*, new subgenus

Diagnosis. — *Proctocaecum* having ratio of body length to width averaging 7.5–15:1* (6).

P. productum (Odhner, 1902) Brooks, 1980

Diagnosis. — With characters of the subgenus.

P. elongatum (Tubangui & Masiluñgen, 1936) Brooks, 1980

Diagnosis. — Ceca opening separately at posterior end of body* (7); maximum body length 7–16 mm* (8); ratio of body length to width averaging more than 20:1 (9).

P. crocodili (Yamaguti, 1954) Brooks, 1980

Diagnosis. — Ceca opening separately at posterior end of body* (7); maximum body length 7–16 mm* (8); forebody less than 10% TBL (10).

P. atae (Tubangui & Masiluñgen, 1936) Brooks, 1980

Diagnosis. — Ceca opening separately at posterior end of body* (7); maximum body length 7–16 mm* (8); ratio of oral sucker width to pharyngeal width 1:0.25–0.40* (11).

P. nicolli Brooks, 1980

Diagnosis. — Ceca opening separately at posterior end of body* (7); maximum body length 7–16 mm* (8); ratio of oral sucker width to pharyngeal width 1:0.25–0.40* (11); vitelline follicles extending anteriorly to posterior margin of acetabulum* (12); maximum oral spine length more than 100 μm * (13).

Genus *Caimanicola*

Teixeira de Freitas & Lent, 1938

(Fig. 7)

Diagnosis. — Acanthostominae having some uterine loops lateral to testes but none posttesticular (8); ceca opening separately and laterally at even levels (9); excretory vesicle Y-shaped with short stem and constriction of arms in middle (14); eggs averaging more than 30 μm long (15); gonotyl lacking* (17); esophagus longer than pharynx (18); tegumental spines unusually robust in mid-forebody (19); maximum body length 7–16 mm* (20).

C. pavidus (Brooks & Overstreet, 1977)
Brooks, 1980

Diagnosis. — Oral spines averaging 25–30 in number* (1).

C. caballeroi (Pelaez & Cruz, 1953) Brooks,
1980

Diagnosis. — Eggs averaging less than 30 μm long (2); maximum body length 2–6 mm (3).

C. marajoarus Teixeira de Freitas & Lent,
1938

Diagnosis. — Eggs averaging less than 30 μm long (2); length of body occupied by uterine loops more than 50% TBL* (4); vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (5).

C. brauni (Mañe-Garzon & Gil, 1961)
Brooks, 1980

Diagnosis. — Eggs averaging less than 30 μm long (2); length of body occupied by uterine loops more than 50% TBL* (4); ratio of oral sucker width to acetabular width 1:0.3–0.7 (6).

Remarks: According to Ostrowski de Nuñez (1984b), *Acanthostomum brauni* of Caballero (1955) is an undetermined species of acanthostome, possibly undescribed.

Genus *Acanthostomum* Looss, 1899

(Figs. 8, 9)

Diagnosis. — Acanthostominae having some uterine loops lateral to testes but none posttesticular (8); ceca opening separately and laterally at even levels (9); eggs averaging more than 30 μm long (15); gonotyl lacking* (17); excretory vesicle with long stem and short arms (21).

Subgenus *Blairium*, new subgenus

Diagnosis. — *Acanthostomum* having ceca opening separately at posterior end of body* (1).

A. scyphocephalum (Braun, 1899) Hughes
et al., 1941

Diagnosis. — With characters of the subgenus.

Remarks: Ostrowski de Nuñez (1986) re-described this species from the type material, which had been missing and presumed lost (see Brooks 1980).

A. americanum (Perez Viguera, 1957) Herber,
1961

Diagnosis. — Length of body occupied by uterine loops more than 50% TBL* (2).

A. megacetabulum Thatcher, 1963

Diagnosis. — Length of body occupied by uterine loops more than 50% TBL* (2); ratio of oral sucker : acetabular width 1:0.8–1.3* (3).

A. gnerii Szidat, 1954

Diagnosis. — Testes oblique (4); vitelline follicles sparse (5).

A. minimum Stunkard, 1938

Diagnosis. — Testes oblique (4); vitelline follicles sparse (5); one cecum atrophied* (6).

A. astorquii Watson, 1976

Diagnosis. — Testes oblique (4); vitelline

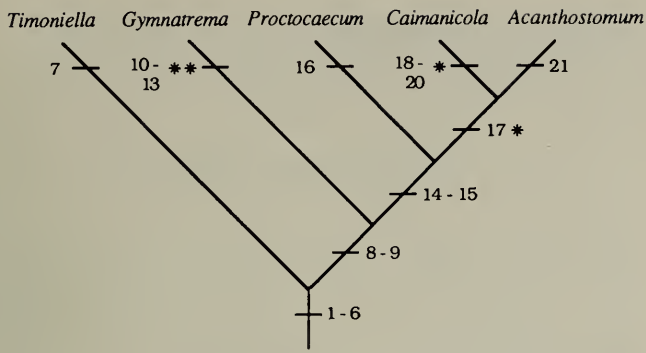


Fig. 4. Phylogenetic relationships among the genera of the subfamily Acanthostominae. Numbers refer to apomorphic traits listed in diagnoses in text. Each asterisk (*) indicates the presence of a homoplasious character; the particular homoplasious characters are denoted by an asterisk in the diagnoses in the text.

follicles sparse (5); one cecum atrophied* (6).

Subgenus *Gibsonium*, new subgenus

Diagnosis.—*Acanthostomum* having vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (7); oral spines averaging less than 20 in number* (8).

A. absconditum (Looss, 1901) Poche, 1926

Diagnosis.—With characters of the subgenus.

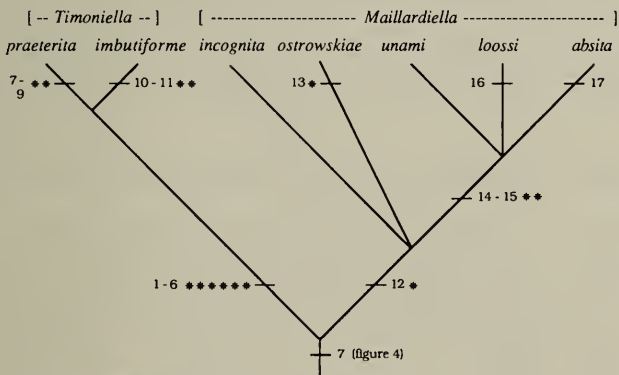


Fig. 5. Phylogenetic relationships among species of *Timoniella*. Numbers refer to apomorphic traits listed in diagnoses in text. Each asterisk (*) indicates the presence of a homoplasious character; the particular homoplasious characters are denoted by an asterisk in the diagnoses in the text.

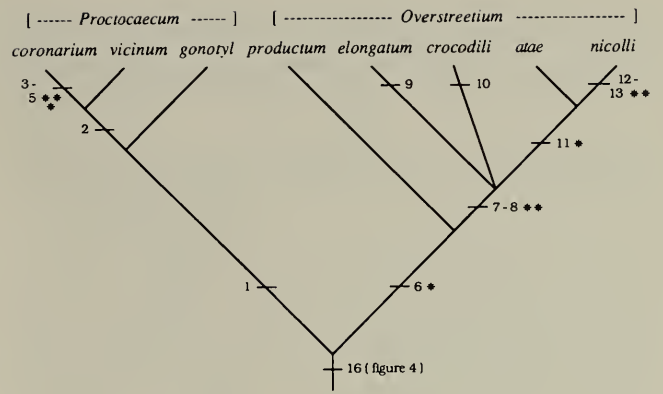


Fig. 6. Phylogenetic relationships among species of *Proctocaecum*. Numbers refer to apomorphic traits listed in diagnoses in text. Each asterisk (*) indicates the presence of a homoplasious character; the particular homoplasious characters are denoted by an asterisk in the diagnoses in the text.

Subgenus *Acanthostomum* Looss, 1899

Diagnosis.—*Acanthostomum* having oral spines averaging 25–30 in number* (9); vitelline follicles extending anteriorly to posterior margin of seminal vesicle* (10); eggs averaging less than 30 μm long (11); cecal bifurcation approximately 10% TBL preacetabular (12).

A. knobus Issa, 1962

Diagnosis.—Ratio of body length to width averaging 7.5–15:1* (13).

A. spiniceps (Looss, 1896) Looss, 1899

Diagnosis.—Ratio of oral sucker width to pharyngeal width 1:0.25–0.40* (14).

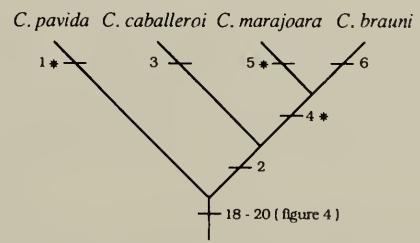


Fig. 7. Phylogenetic relationships among species of *Caimanicola*. Numbers refer to apomorphic traits listed in diagnoses in text. Each asterisk (*) indicates the presence of a homoplasious character; the particular homoplasious characters are denoted by an asterisk in the diagnoses in the text.

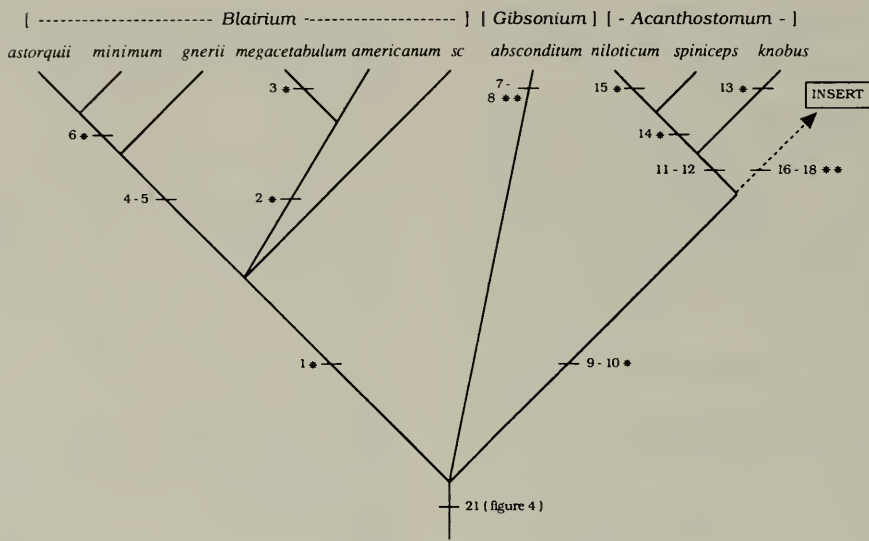


Fig. 8. Phylogenetic relationships among species of *Acanthostomum* excluding *Acanthostomum* (*Atrophecaecum*). Numbers refer to apomorphic traits listed in diagnoses in text. Each asterisk (*) indicates the presence of a homoplasious character; the particular homoplasious characters are denoted by an asterisk in the diagnoses in the text.

A. niloticum Issa, 1962

Diagnosis. — Ratio of oral sucker width to pharyngeal width 1:0.25–0.40* (14); vitelline follicles extending anteriorly to posterior margin of acetabulum* (15).

terior margin of seminal vesicle* (10); vitelline follicles terminating preovarially (16); length of body occupied by uterine loops more than 50% TBL* (17); forebody 10–20% TBL* (18).

Subgenus *Atrophecaecum* Bhalerao, 1940

Diagnosis. — *Acanthostomum* having oral spines averaging 25–30 in number* (9); vitelline follicles extending anteriorly to pos-

A. indicum Sinha, 1942

Diagnosis. — With characters of the subgenus.

A. slusarskii Kalyankar, 1977

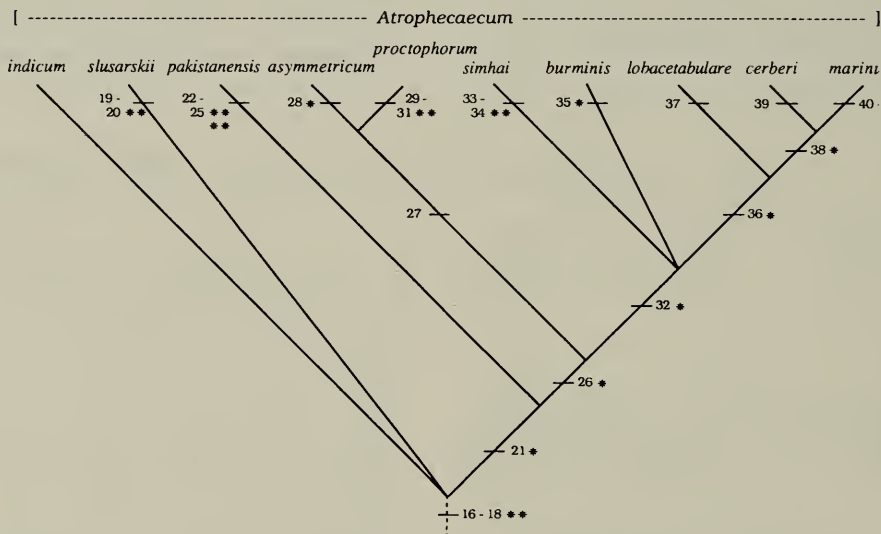


Fig. 9. Phylogenetic relationships among species of *Acanthostomum* (*Atrophecaecum*). Numbers refer to apomorphic traits listed in diagnoses in text. Each asterisk (*) indicates the presence of a homoplasious character; the particular homoplasious characters are denoted by an asterisk in the diagnoses in the text.

Diagnosis. —Ceca opening into excretory vesicle* (19); maximum body length 7–16 mm* (20).

A. pakistanense Coil & Kuntz, 1960

Diagnosis. —Prepharynx shorter than pharynx* (21); forebody 10–20% TBL* (22); ratio of body length to width averaging 7.5–15:1* (23); oral spines averaging 20–24 in number* (24); maximum oral spine length more than 100 μm * (25).

A. asymmetricum (Simha, 1958) Khalil, 1963

Diagnosis. —Prepharynx shorter than pharynx* (21); one cecum lost (27); maximum body length 7–16 mm* (28).

A. proctophorum (Dwivedi, 1966) Yamaguti, 1971

Diagnosis. —Prepharynx shorter than pharynx* (21); one cecum lost (27); length of body occupied by uterine loops more than 50% TBL* (29); oral spines averaging 20–24 in number* (30); vitelline follicles confluent preovarially (31).

A. simhai Khalil, 1963

Diagnosis. —Prepharynx shorter than pharynx* (21); one cecum atrophied* (26); vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (32); ratio of body length to width averaging 7.5–15:1* (33); maximum body length 7–16 mm* (34).

A. burminis (Bhalerao, 1926) Bhalerao, 1936

Diagnosis. —Prepharynx shorter than pharynx* (21); one cecum atrophied* (26); vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (32); length of body occupied by uterine loops more than 50% TBL* (35).

A. lobacetabulare Brooks & Caira, 1982

Diagnosis. —Prepharynx shorter than pharynx* (21); one cecum atrophied* (26); vitelline follicles not extending anteriorly to

posterior margin of seminal vesicle* (32); subterminal mouth* (36); lobate acetabulum (37).

A. cerberi (Fischthal & Kuntz, 1965) Brooks & Caira 1982

Diagnosis. —Prepharynx shorter than pharynx* (21); one cecum atrophied* (26); vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (32); subterminal mouth* (36); no oral spines* (38); no esophagus (39).

A. marinum (Coil & Kuntz, 1960) Brooks & Caira, 1982

Diagnosis. —Prepharynx shorter than pharynx* (21); one cecum atrophied* (26); vitelline follicles not extending anteriorly to posterior margin of seminal vesicle* (32); subterminal mouth* (36); no oral spines* (38); no prepharynx (40); secondary group of vitelline follicles surrounding testes (41).

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(DRB) Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1 Canada; (BH) Laboratorio de Zoologia Invertebrados, Facultad de Ciencias, Uni-

versidad de la Republica, Tristan Narvaja 1674, 11200 Montevideo, Uruguay.

Appendix 1

Transformation series for characters used to formulate phylogenetic hypotheses for acanthostome digeneans (for outgroup argumentation, see Brooks 1980, Brooks & Caira 1982, Brooks et al. 1985, Brooks et al. 1989). 0 = plesiomorphic; 1 or higher indicates apomorphic states. *U* = nonlinear transformation series, run unordered in computer-assisted analyses (numbers assigned to each apomorphic state are arbitrary).

1. Oral sucker subterminal (0); terminal (1).
2. Oral sucker lacking spines (0); armed with single row of spines (1).
3. Preacetabular pit lacking (0); present (1).
4. Ventrogenital pit present (0); lacking (1).
5. Genital pore in preacetabular pit (0); not in preacetabular pit (1).
6. Seminal vesicle not coiled posteriorly (0); coiled posteriorly (1).
7. Gonotyl lacking (0); suckerlike (1); large, solid-muscular (2). *U*
8. Seminal receptacle postovarian (0); preovarian (1).
9. Vitelline follicles extending anteriorly to posterior margin of seminal vesicle (0); not extending anteriorly to posterior margin of seminal vesicle (1); confluent dorsally (2); confluent posttesticularly (3). *U*
10. Space occupied by uterine loops less than 45% TBL (0); more than 50% TBL (1).
11. Prepharynx longer than pharynx (0); shorter than pharynx (1).
12. Ratio of oral sucker width to pharyngeal width averaging 1:0.5 (0); 1:0.25–0.40 (1).
13. Ratio of body length to width averaging less than 7.5:1 (0); 7.5–15:1 (1); more than 20:1 (2). *U*
14. Ceca ending blindly near posterior end of body (0); cyclocoel (1); opening separately at posterior end of body (2); opening into excretory vesicle (3); opening separately and laterally at even levels (4); one cecum atrophied (5); one cecum opening laterally and one cecum ending blindly (6); opening separately and laterally at uneven levels (7); one cecum lost (8). *U*
15. Forebody more than 20% TBL (0); 10–20% TBL (1); less than 10% TBL (2).
16. Maximum body length less than 7 mm (0); 7–16 mm (1).
17. Ratio of oral sucker : acetabular width 1:0.6–0.9 (0); 1:0.8–1.3 (1); 1:0.3–0.7 (2).
18. Oral spines averaging 20–24 in number (0); 25–30 (1); less than 20 (2). *U*
19. No constriction in seminal vesicle (0); constriction present (1).
20. Posttesticular loops present (0); some uterine loops lateral to testes but none posttesticular (1).
21. Excretory vesicle Y-shaped with long stem (0); with short stem and constriction of arms in middle (1); long stem and short arms (2).
22. Eggs averaging less than 30 μm long (0); more than 30 μm long (1).
23. Maximum oral spine length less than 100 μm long (0); more than 100 μm long (1).
24. Esophagus shorter than pharynx (0); longer than pharynx (1).
25. Tegumental spines not unusually robust in mid-forebody (0); unusually robust in mid-forebody (1).
26. Testes tandem (0); oblique (1).
27. Vitelline follicles numerous (0); sparse (1).
28. Cecal bifurcation averages 20% TBL preacetabular (0); 10% TBL preacetabular (1).
29. Vitelline follicles terminating at least at ovarian level and no further posterior than posterior margin of the ovary (0); extending posteriorly to middle of posterior testis (1); terminating preovarially (2). *U*
30. Vitelline follicles not confluent preovarially (0); confluent preovarially (1).
31. Acetabulum not lobate (0); lobate (1).
32. Esophagus present (0); lacking (1).
33. Prepharynx present (0); lacking (1).
34. Secondary group of vitelline follicles surrounding testes lacking (0); present (1).